

Size-assortative mate selection and molting increment of *Scylla* mud crabs in wild coastal mangrove habitats



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Abstract Size-assortative, nonrandom mate selection and periodic molting for growth, development, and reproduction have been observed in animals, including brachyuran crabs. This study investigated the mate selection of *Scylla olivacea* from four wild habitats in the Bay of Bengal, Bangladesh, and the molting dynamics of *Scylla* species in coastal mangroves of Pattani Bay, Thailand. A total of 34 pairs of *S. olivacea* were collected from four habitats in the Meghna Estuary, where 29 pairs (85%) of males were larger than 5 pairs (15%) of females. A higher abundance of mating pairs was observed in the rainy season (higher temperature and lower salinity) than in the winter season (lower temperature and higher salinity). Significant differences between sexes were found in carapace width (CW), internal carapace width (ICW), carapace length (CL), and body weight (BW). Male size and BW were significantly correlated with female sex. Morphometric traits differed significantly across habitats and seasons. The most frequent CW size class was 8.5–9.0 cm for males (34.3%) and 7.5–8.0 cm for females (26.5%). During molting, *S. olivacea* and *S. paramamosain* presented increases by 1.28 ± 0.48 and 1.35 ± 0.18 cm (CW), 0.93 ± 0.33 and 0.83 ± 0.15 cm (CL), and 0.54 ± 0.19 and 0.45 ± 0.17 cm (BH), respectively. No significant differences in molting increment were detected between species or sexes. Premolt size was positively correlated with increment but negatively correlated with percentage increment. These findings offer valuable biological insights for the ecological management and aquaculture practices of *Scylla* mud crabs.

Keywords: mud crab, mate choice, increment, bay of bengal, pattani bay

1. Introduction

Nonrandom sexual mate selection has been observed among individuals, emphasizing the importance of understanding the underlying processes that drive assortative mating and the evolutionary mechanisms shaping mate choice in natural populations (Dennenmoser et al., 2020; Fazhan et al., 2017b; Tina & Muramatsu, 2020). Nonrandom mate selection has been reported not only across diverse animal groups (Frommen & Bakker, 2006; Ng & Williams, 2014; Tsuji et al., 2000) but also in brachyuran crabs, where size-assortative pairing represents a common feature of nonrandom mating (Clark & Backwell, 2016; Fazhan et al., 2017b; Sal Moyano et al., 2014; Tina et al., 2018; Waiho et al., 2015).

Sexual selection is a key driver of assortative mating, ensuring greater potential for mating success in many species, including brachyuran crabs (Clark & Backwell, 2016; Dennenmoser et al., 2020; Fazhan et al., 2017b; Sal Moyano et al., 2014). The criteria for sexual selection between males and females have been extensively documented in brachyuran crabs. For example, females select mates on the basis of burrow characteristics (length and depth) in the fiddler crabs *Austruca perplexa* (Tina & Muramatsu, 2022) and *Uca beebei* (Christy, 1987). Similarly, large unmated males of the semiterrestrial crab *Neohelice granulata* release chemical signals to attract females (Sal Moyano et al., 2014), whereas body size influences female choice in the grapsid crab *Gaetice depressus* (Fukui, 1995). In addition, claw size and waving displays play significant roles in mate selection in the fiddler crabs *Uca tangeri* (Oliveira & Custódio, 1998) and *Austruca perplexa* (Tina & Muramatsu, 2022). Male mate choice has also been reported in some species. For example, females release pheromones to attract males in the spider crab *Inachus dorsettensis* (Christy & Wada, 2015; Jones & Hartnoll, 1997). Body size serves as another criterion, as males preferentially select larger females in the fiddler crab *Uca mjoebergi* (Christy & Wada, 2015; Reading & Backwell, 2007) and in the mud crab *Scylla* spp. (Fazhan et al., 2017b; Waiho et al., 2015).

The mud crab genus *Scylla* (family: Portunidae) is widely distributed across tropical to warm temperate Indo-Pacific regions, where it represents a major fishery resource primarily associated with mangrove forests and estuaries (Keenan et al., 1998; Lovatelli et al., 2025; Meynecke et al., 2012; Pati et al., 2023). Juveniles are predominantly associated with mangrove areas, whereas adults and subadults generally occupy intertidal and subtidal mudflats along the mangrove fringe (Alberts-

Hubatsch et al., 2016; Pati et al., 2023). Within these habitats, burrows serve as permanent shelters for subadult and adult crabs in the intertidal zone (Ewel et al., 2009; Leoville et al., 2021). Burrowing is a common behavioral trait among benthic invertebrates inhabiting marine, estuarine, and freshwater sediments (Kuhapong et al., 2021; Maheta & Vachhrajani, 2023).

Four species of *Scylla* are currently recognized: *S. serrata*, *S. olivacea*, *S. paramamosain*, and *S. tranquebarica* (Keenan et al., 1998). Among them, *S. olivacea* dominates wild harvests in Bangladesh (Rouf et al., 2016; Sarower et al., 2017) and aquaculture production, ranking as the second most valuable export crustacean after shrimp (Islam et al., 2024; Rahman et al., 2017; Rouf et al., 2021). In Thailand, *S. olivacea* is also most abundant, followed by *S. paramamosain* and *S. tranquebarica* (Islam et al., 2025; Lovatelli et al., 2025; Mae et al., 2025). The high market demand for protein-rich meat has driven the rapid expansion of fattening and soft-shell farming in several countries, although reliance on wild-caught juveniles persists owing to limited hatchery and rearing technologies (Alberts-Hubatsch et al., 2016; Ali et al., 2020; Islam et al., 2024; Pati et al., 2023; Rahman et al., 2017; Rouf et al., 2021; Waiho et al., 2015). Ecological interactions between mud crabs and their environment play a pivotal role throughout their life cycle and strongly influence key biological behaviors, including migration, reproduction, and breeding (Fazhan et al., 2017a; Pati et al., 2023). The life cycle of mud crabs consists of three major stages: larval (dispersing), juvenile (benthic), and adult (Alberts-Hubatsch et al., 2016; Pati et al., 2023). During the juvenile stage, mud crabs migrate from marine waters to estuaries, where they mature and inhabit muddy mangrove forests characterized by fluctuating temperatures and salinities (Alberts-Hubatsch et al., 2016; Fazhan et al., 2017a; Pati et al., 2023; Vay, 2001).

The physiology of *Scylla* spp., including growth, molting, metabolism, and survival, is strongly influenced by physicochemical parameters such as temperature, salinity, and rainfall (Fazhan et al., 2017a; Liu et al., 2022a; Pati et al., 2023; Zhang et al., 2022). Mud crabs tolerate water temperatures of 18–31 °C and salinities of 1–33 ppt, with optimal growth reported at 27–30 °C (Pati et al., 2023; Syafaat et al., 2021). For example, the preferred egg incubation temperature for *S. olivacea* is 28–30 °C (Ikhwanuddin et al., 2015), while *S. paramamosain* exhibits reduced growth and survival at both lower (24 °C) and higher (32 °C) temperatures compared to 28 °C (Syafaat et al., 2021). Similarly, the egg incubation period of *S. serrata* decreases from 30 to 10 days as temperature increases from 20.3 °C to 30 °C under captive conditions (Hamasaki, 2003). Salinity also influences physiological performance; for instance, metabolic activity in *S. serrata* increases as salinity rises from 10 to 35 ppt (Pati et al., 2023), while higher salinity enhances egg development in *S. olivacea* (Amin-Safwan et al., 2019). Their nocturnal feeding habits and burrowing behavior allow them to use burrows as refuges from predators and as sites for key biological processes such as molting and reproduction in subtidal and mangrove habitats (Ewel et al., 2009; Pati et al., 2023; Sal Moyano et al., 2012; Skov et al., 2002; Tina et al., 2018). However, there is currently no direct evidence that mud crabs specifically use burrows as mating shelters or how this behavior interacts with environmental conditions.

Knowledge of mating behavior is a key component of understanding the biology of any organism. In mud crabs, mating typically occurs in intertidal coastal zones and estuaries before females migrate up to 50 km offshore to spawn (Koolkalya et al., 2016; Waiho et al., 2015). Their mating strategy involves distinct courtship phases: prolonged precopulatory, molting, copulation, and postcopulatory (Fazhan et al., 2017b; Waiho et al., 2015). Previous research has addressed aspects of *Scylla* reproductive biology, including the spawning traits of berried females (Alberts-Hubatsch et al., 2016; Hewitt et al., 2022; Koolkalya et al., 2016; Pati et al., 2023), laboratory mating experiments (Asmat-Ullah et al., 2021; Fazhan et al., 2017b; Waiho et al., 2015), and courtship observations of wild-caught individuals via gill nets (Fazhan et al., 2017b). However, mating and sexual selection within natural burrow habitats have not yet been documented. Knowledge of size-assortative mating in *S. olivacea* indicates a non-random mating pattern in both natural and captive conditions, where individuals select partners of similar body size. Specifically, larger males tend to mate with larger females, whereas smaller males pair with smaller females (Fazhan et al., 2017b; Waiho et al., 2015). Moreover, reproductive performance, particularly spawning and hatching success, is positively associated with larger female size in *S. olivacea*, suggesting that larger females contribute more effectively to seed production (Asmat-Ullah et al., 2021, 2025). This evidence supports the preferential selection of larger broodstock individuals in hatchery and aquaculture programs (Asmat-Ullah et al., 2025, 2021). In addition, size at mating and size at sexual maturity are critical biological parameters that inform fisheries management and aquaculture practices. These metrics are essential for establishing minimum legal size limits, size-based stocking strategies, and optimizing broodstock selection for aquaculture systems, including grow-out farming, fattening, and soft-shell crab production (Ali et al., 2020; Asmat-Ullah et al., 2025).

Molting, which is regulated by ecdysteroid hormones, is a fundamental process linking growth, development, and reproduction in crustaceans (Gong et al., 2015; LeBlanc, 2007). In mud crabs, shell replacement is essential for growth, reproduction, and survival, yet individuals are highly vulnerable to predation and cannibalism during molting, often seeking refuge in burrows as a defensive strategy (Fazhan et al., 2017b; Serdiati et al., 2025; Waiho et al., 2015). Although several laboratory studies have examined molting dynamics in mud crabs (Fazhan et al., 2017b; Gong et al., 2015; Nurcahyono et al., 2024; Serdiati et al., 2025; Tahya et al., 2016), molting behavior under natural conditions remains poorly understood, largely because ecdysteroid hormones are unstable and sensitive to environmental variability in the wild.

Therefore, this study investigated the mating choices of *S. olivacea* in natural coastal mangrove habitats in the Meghna estuary Islands in the Bay of Bengal, Bangladesh. In addition, we examined the molting dynamics and growth increments of mud crabs from Pattani Bay, Thailand.

2. Materials and Methods

2.1. Sampling sites

2.1.1. Bay of bengal

An estuary is defined as a semienclosed water body with a connection to the sea (Shaha et al., 2022). The Meghna Estuary, located at the easternmost margin of the Ganges Delta, lies east of Hatia Island, east of Bhola, north of Noakhali, and south of the Bay of Bengal (Figure 1a). The lower Meghna River estuary is a vital breeding and nursery habitat for freshwater, brackish, and marine fisheries, supporting the livelihoods of local communities (Rahman et al., 2022; Shaha et al., 2022). In addition to its ecological functions, the Meghna Estuary has considerable economic importance because of its contributions to fisheries, aquaculture, and mangrove ecosystems. Its ecological dynamics are strongly influenced by three distinct seasons: the monsoon season (June–October), postmonsoon season (November–February), and premonsoon season (March–May) (Hossain et al., 2012; Sarker, 2021). The hydrology, water parameters, and primary productivity of the Meghna River Basin are largely regulated by the wet season, which is characterized by heavy rainfall and substantial river discharge (Shaha et al., 2022). The mud crab *S. olivacea* is widely distributed across various islands of the Meghna Estuary and other coastal regions of Bangladesh (Rouf et al. 2016; Ali et al. 2020; Rouf et al. 2021; Islam et al. 2024). For the present study, four seaside island habitats were selected for sampling wild-mating *S. olivacea*: Char Pataliya (CP, Longitude: 90.88658, Latitude: 22.08591), Nijhum Dwip (ND, Longitude: 90.960694, Latitude: 22.049389), Char Nizam (CN, Longitude: 90.841583, Latitude: 21.963806), and Knife Island (KI, Longitude: 90.815111, Latitude: 21.960194) (Figure 1a).

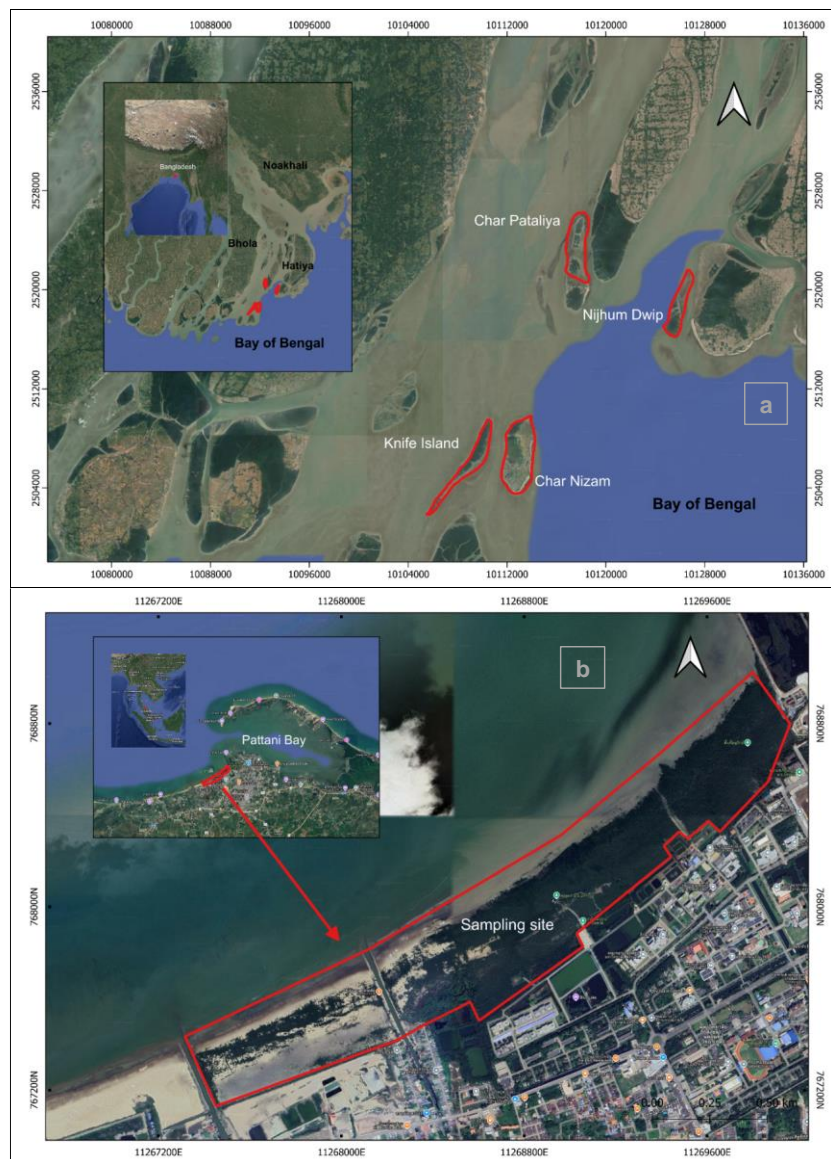


Figure 1 Sampling locations of *S. olivacea* mates on different islands of the Meghna Estuary in the Bay of Bengal, Bangladesh (a), and molted *Scylla* mud crab from Pattani Bay (b), Thailand.

2.1.2. Pattani bay

This study was conducted in the coastal mangrove ecosystem areas of Pattani Bay in the southern Gulf of Thailand (Figure 1b). Pattani Bay is a semienclosed shallow estuarine covering 74 sq. km and a 12 km long sandpit on the northeast side (Hajisamae et al., 2025). The sand and muddy sand coastal zones of Pattani Bay are associated with different mangrove vegetation and aquatic and terrestrial organisms (Kaewtubtim et al., 2017). *Scylla* mud crab species, *S. olivacea*, *S. paramamosain*, and *S. tranquebarica* are fished in the coastal mangrove ecosystem in Pattani Bay (Lovatelli et al., 2025; Maae et al., 2025; Soe et al., 2024). The Pattani Bay mangrove ecosystem is estimated to cover 900 ha and consists of different types of plant species, whereas the two dominant species are *Avicennia marina* and *Rhizophora mucronata* (Hajisamae et al., 2025; Hajisamae & Yeemin, 2014; Kaewtubtim et al., 2017).

2.2. Sampling procedure and data record

2.2.1. Biometeorological data record

The real-time monthly sea surface temperature (SST; *sst.surftemp*) was collected from four habitats of the Bay of Bengal during both the rainy season (July–August) and the winter season (January–February) (Embury et al., 2024). In addition, data on air temperature, water salinity, rainfall, and water discharge from upstream to downstream of the Meghna Estuary during these two seasons were obtained from secondary sources (Sarker et al., 2021; Shaha et al., 2022).

2.2.2. Mating

Mates of *Scylla olivacea* were collected from July–August 2023 and January–February 2024 with local harvesters using rods and spades to extract crabs from burrows. Male–female pairs were tied, placed in labeled polyethylene bags, and transported in iceboxes. Only pairs in which the male held the female in the guarding position were considered (Asmat-Ullah et al., 2021; Fazhan et al., 2017b; Waiho et al., 2015). The samples were anesthetized and preserved for further laboratory analysis. Species and sex were identified following Keenan et al. (1998). Carapace width (CW), internal carapace width (ICW), and carapace length (CL) were measured to the nearest 0.01 cm via a Vernier caliper, and body weight (BW) was measured to the nearest 0.01 g via an electronic balance.

The mating stage was then confirmed. Completion of copulation in males was identified by the presence of scratches on the first pair of walking legs caused by rubbing against the female's carapace during the precopulatory embrace (Fazhan et al., 2017b; Ikhwanuddin et al., 2011; Waiho et al., 2015). The mating status of the females was assessed on the basis of carapace conditions and morphological characteristics. Newly mated females presented a soft carapace, widened genital openings from gonopod insertion, a darkened and broadened abdominal flap, and two groove-like depressions resulting from pressure from the male pleopods. In contrast, unmated or immature females have a hard carapace, a bright intermediate abdominal flap, and narrow gonopores (Ali et al., 2020; Fazhan et al., 2017b; Ikhwanuddin et al., 2011; Waiho et al., 2015). Male maturity was verified by dissecting individuals and visually assessing the presence or absence of spermatozoa (Mhd et al., 2018). Female maturity was determined through examination of the abdominal flap and the gonadal development stage (Ikhwanuddin et al., 2011). In this study, only *S. olivacea* pairs observed at the precopulation stage were included to examine patterns of mate choice, while mature male mates with unmated females were considered for data collection. Most female juvenile mates recorded in this study were expected to undergo a pubertal molt, confirming that they were unmated (Waiho et al., 2015).

2.2.3. Molting

Field sampling was conducted from July to December 2023 in the coastal zone of Pattani Bay. A local expert mud crabber was employed to locate and extract crabs from burrows via a rod and spade. Newly molted crabs with intact premolt exoskeletons were targeted for this experiment. The species and sex of each individual were identified via the guidelines of the morphometric characteristics of the *Scylla* mud crab (Keenan et al., 1998). The carapace width (CW), carapace length (CL), and body height (BH) of both the premolt exoskeleton and the postmolt crab were measured to the nearest 0.01 cm using a Vernier caliper. After the measurements, all the crabs were released back into the wild.

2.3. Statistical analysis

All the data were analyzed via Microsoft Excel and SPSS v.21. Prior to analysis, the data were normalized via $\log(x+1)$ transformation. Student's *t* tests were used to assess differences in carapace width (CW), carapace length (CL), internal carapace width (ICW), and body weight (BW) between males and females. One-way ANOVA was used to test habitat-related variations in CW, CL, ICW, and BW separately for males and females, followed by Tukey's post hoc tests to identify pairwise habitat differences. Seasonal variation in the morphometric traits of males and females was also evaluated via *t* tests. However, sea surface temperatures across four different habitats during the rainy and winter seasons were analyzed using a two-way ANOVA with replication.

Carapace width was grouped into 0.5 cm intervals to determine the peak frequency and percentage distribution of male and female mates. Correlations were performed between male and female mates for CW–CW, ICW–ICW, CL–CL, and BW–BW to examine size-assortative mating. For the molting data, t tests were used to compare increases in CW, CL, and BH between species and sexes. Correlation analyses were conducted on absolute and percentage increments of each parameter (CW, CL, BH).

3. Results

3.1. Biometeorological parameters

The minimum, maximum, mean, and standard deviation (SD) of water temperature are presented in Table 1. Water temperature was significantly higher during the rainy season compared to the winter season ($p < 0.05$, ANOVA), whereas no significant difference was observed among habitats ($p > 0.05$, ANOVA). In addition, salinity, rainfall, water discharge, and air temperature are summarized in Table 2. Salinity was higher in the winter season and lower in the rainy season, with values generally increasing from upstream to downstream. Higher rainfall, water discharge, and air temperature were recorded during the rainy season (1800 mm, 82,000 m³ s⁻¹, and 28.3 °C, respectively), whereas lower values were observed in the winter season (37 mm, <10,000 m³ s⁻¹, and 20.64 °C, respectively).

Table 1 Descriptive statistics of surface water temperature across two seasons at four sampling stations in the Bay of Bengal, Bangladesh.

Habitats	Temperature (°C)							
	Rainy season				Winter season			
	Min	Max	Mean	SD	Min	Max	Mean	SD
Char Pataliya (CP)	29.20	29.72	29.39	0.21	21.95	22.52	22.27	0.19
Nijhum Dwip (ND)	29.20	29.72	29.39	0.21	22.01	22.56	22.33	0.19
Char Nizam (CN)	29.23	29.76	29.42	0.21	22.11	22.67	22.43	0.19
Knife Island (KI)	29.24	29.77	29.43	0.21	22.11	22.67	22.42	0.19

Source: Embury et al. (2024).

Table 2 Statistical summary of water environmental parameters (water and air temperature, salinity), river discharge, and rainfall across the rainy and winter seasons in the Meghna Estuary, Bay of Bengal, Bangladesh.

Parameters	Rainy season				Dry Season				References
	HI	LE	CK	Mean	HI	LE	CK	Mean	
Water temperature (°C)	-	-	-	29.41	-	-	-	22.36	Present study (Shaha et al., 2022)
	30.5	29.8	30.1	30.13	22	22.9	23.1	22.67	
Salinity (psu)	0.08	0.09	0.48	0.22	7	12.2	12.4	10.53	
Discharge water (m ³ s ⁻¹)	-	-	-	82000	-	-	-	< 10,000	
Air temperature (°C)	-	-	-	28.3	-	-	-	20.64	(Sarker, 2021)
Rainfall (mm)	-	-	-	1800	-	-	-	37	

Note: HI; Hatia Island, LE; Charfasson; and CK; Char Kukrimukri (Upstream to downstream = HI→LE→CK).

3.2. Mating

A total of 34 pairs of *S. olivacea* were collected from four habitats in the Meghna Estuary, Bay of Bengal; 24 pairs were collected during the rainy season (July–August 2023), and 10 pairs were collected during the winter season (January–February 2024) (Table 3). In 29 pairs (85%), males were larger than females were, whereas females were larger in 5 pairs (15%). For male mates, the carapace width (CW) ranged from 6.87 to 10.50 cm (mean \pm SD: 8.78 \pm 0.89 cm), the internal carapace width (ICW) ranged from 6.65 to 10.12 cm (8.45 \pm 0.83 cm), the carapace length (CL) ranged from 4.80 to 7.30 cm (6.22 \pm 0.59 cm), and the body weight (BW) ranged from 68.57 to 272.16 g (160.67 \pm 49.09 g). For female mates, the CW ranged from 5.54 to 9.70 cm (7.55 \pm 0.10 cm), the ICW ranged from 5.31 to 9.30 cm (7.20 \pm 0.89 cm), the CL ranged from 3.80 to 6.90 cm (5.27 \pm 0.70 cm), and the BW ranged from 31.02 to 147.28 g (80.47 \pm 26.35 g). Male and female pairs presented significant differences in carapace width (CW), internal carapace width (ICW), carapace length (CL), and body weight (BW) (t test, $p < 0.001$) (Table 4). Male size (CW, ICW, CL) and BW were also significantly correlated with female values (CW–CW: $R^2 = 0.25$, $p < 0.001$; ICW–ICW: $R^2 = 0.28$, $p < 0.001$; CL–CL: $R^2 = 0.13$, $p < 0.001$; BW–BW: $R^2 = 0.33$, $p < 0.001$) (Figure 2).

Table 3 Estimated carapace width (CW), carapace length (CL), internal carapace width (ICW), and body weight (BW) of male and female mates of *S. olivacea* mud crab from different Meghna Estuary Islands in the Bay of Bengal, Bangladesh.

Factors	Sex	n	Morphometric measurement							
			CW (cm)		ICW (cm)		CL (cm)		BW (gm)	
Habitats			Min–Max	Ave ± SD	Min–Max	Ave ± SD	Min–Max	Ave ± SD	Min–Max	Ave ± SD
Knife Island (KI)	Male	19	7.90-10.30	9.02±0.68	7.60-9.60	8.64±0.62	5.50-7.10	6.33±0.49	113.36-231.70	171.41±39.83
	Female		6.10-9.70	7.83±0.96	5.80-9.30	7.44±0.88	4.20-6.90	5.46±0.68	39.88-147.28	86.09±26.09
Char Nizam (CN)	Male	7	6.90-10.50	8.93±1.15	6.65-10.12	8.66±1.09	4.80-7.10	6.14±0.82	71.97-272.16	169.32±66.66
	Female		6.51-7.92	7.41±0.53	6.22-7.60	7.09±0.50	4.50-5.60	5.18±0.42	50.89-96.50	74.79±18.56
Nijhum Dwip (ND)	Male	4	8.59-9.00	8.79±0.22	8.28-8.70	8.50±0.24	6.05-6.50	6.26±0.22	130.52-190.23	161.11±24.79
	Female		7.30-8.88	7.96±0.75	7.00-8.34	7.56±0.63	5.10-6.28	5.57±0.54	73.24-117.21	96.86±18.91
Char Pataliya (CP)	Male	4	6.87-7.83	7.38±0.42	6.70-7.65	7.13±0.43	4.96-6.77	5.79±0.77	68.57-125.61	95.10±26.06
	Female		5.54-6.67	6.08±0.54	5.31-6.48	5.89±0.59	3.80-4.56	4.21±0.37	31.02-75.40	47.33±20.18
Season										
Rainy season	Male	24	8.22-10.30	9.06±0.57	7.72-9.60	8.72±0.50	5.50-7.10	6.34±0.44	113.36-231.70	173.60±36.28
	Female		6.50-9.70	7.87±0.83	6.29-9.30	7.49±0.75	4.50-6.90	5.47±0.60	51.40-147.28	87.82±23.78
Winter season	Male	10	6.87-10.50	8.11±1.16	6.65-10.12	7.81±1.12	4.80-7.30	5.92±0.79	68.57-272.16	129.65±62.93
	Female		5.54-8.20	6.79±0.92	5.31-7.60	6.51±0.84	3.80-5.65	4.79±0.73	31.02-96.50	62.83±24.70
Overall	Male	34	6.87-10.50	8.78±0.89	6.65-10.12	8.45±0.83	4.80-7.30	6.22±0.59	68.57-272.16	160.67±49.09
	Female		5.54-9.70	7.55±0.10	5.31-9.30	7.20±0.89	3.80-6.90	5.27±0.70	31.02-147.28	80.47±26.35

Table 4 Statistical analysis of intrasex male and female mates in different habitats (ANOVA) and seasons (t test) and intersex mates (t test) on the basis of the length (CW, ICW, CL) and weight (BW) variables of *S. olivacea* in the Bay of Bengal.

Parameter	Sex	Habitats	Season
	Intrasex	df	p value
CW	Male (♂)	3	< 0.01
	Female (♀)	3	< 0.01
ICW	Male (♂)	3	< 0.01
	Female (♀)	3	< 0.01
CL	Male (♂)	3	> 0.05
	Female (♀)	3	< 0.01
BW	Male (♂)	3	< 0.01
	Female (♀)	3	< 0.01
Between sex	Inter sex		p value
CW	♀♂		< 0.001
ICW	♀♂		< 0.001
CL	♀♂		< 0.001
BW	♀♂		< 0.001

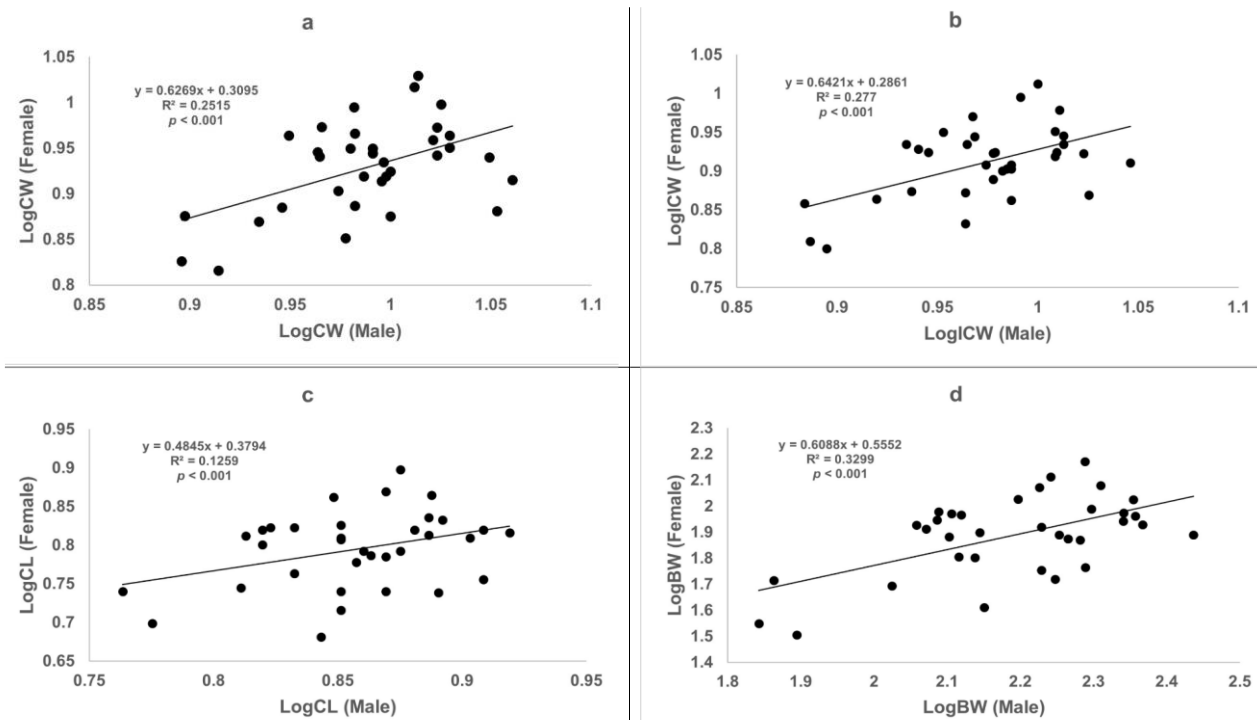


Figure 2 Correlations between male–female length (CW = a, ICW = b, CL = c) and body weight (BW = d) of *S. olivacea* mud crabs from the Bay of Bengal, Bangladesh.

3.2.1. Peak size of mating

Among the CW size classes, the highest percentage size class for males was 8.5–9.0 cm (12 individuals, 34.3%), whereas for females, it was 7.5–8.0 cm (9 individuals, 26.5%) (Figure 3). The percentage of individuals gradually increased from the smallest size classes to these peak classes and then gradually decreased in the larger size classes.

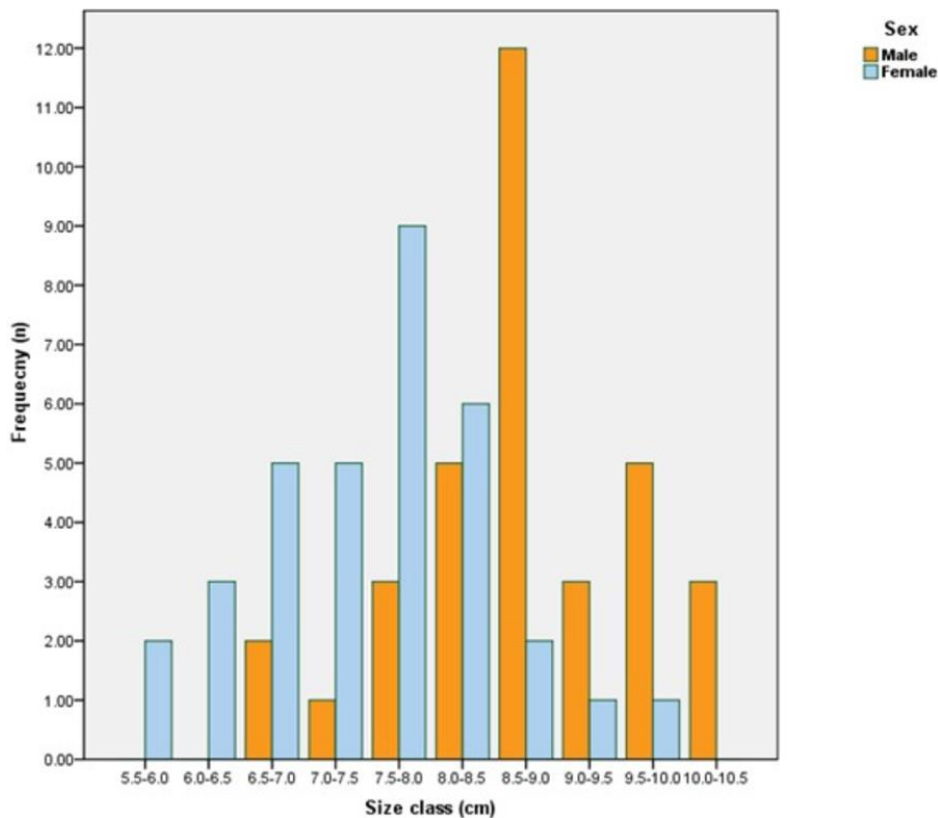


Figure 3 Frequencies of male and female *S. olivacea* mates in different size classes on the basis of carapace width (CW) from the Bay of Bengal.



3.2.2. Effects of habitats

Both sexes presented significant differences in CW, ICW, and BW across habitats (ANOVA, $p < 0.01$), except for CL ($p > 0.05$) (Table 4, Figure 4a-b). Male crabs were the most common on Knife Island (KI), followed by Char Nizam (CN), Nijhum Dwip (ND), and Char Pataliya (CP), with mean CWs of 9.02 ± 0.68 cm, 8.93 ± 1.15 cm, 8.79 ± 0.22 cm, and 7.38 ± 0.42 cm; ICWs of 8.64 ± 0.62 cm, 8.66 ± 1.09 cm, 8.50 ± 0.24 cm, and 7.13 ± 0.43 cm; CLs of 6.33 ± 0.49 cm, 6.14 ± 0.82 cm, 6.26 ± 0.22 cm, and 5.79 ± 0.77 cm; and BWs of 171.41 ± 39.83 g, 169.32 ± 66.66 g, 161.11 ± 24.79 g, and 95.10 ± 26.06 g, respectively (Table 3). The greatest number of female crabs were subjected to ND, followed by KI, CN, and CP, with mean CWs of 7.96 ± 0.75 cm, 7.83 ± 0.96 cm, 7.41 ± 0.53 cm, and 6.08 ± 0.54 cm; ICWs of 7.56 ± 0.63 cm, 7.44 ± 0.88 cm, 7.09 ± 0.50 cm, and 5.89 ± 0.59 cm; CLs of 5.57 ± 0.54 cm, 5.46 ± 0.68 cm, 5.18 ± 0.42 cm, and 4.21 ± 0.37 cm; and BWs of 96.86 ± 18.91 g, 86.09 ± 26.09 g, 74.79 ± 18.56 g, and 47.33 ± 20.18 g, respectively. Both the size (CW, ICW) and weight (BW) of both sexes significantly differed between CP habitat mates and the other three habitats (Tukey's test, $p < 0.05$). However, no significant variation was detected among mates from KI, CN, and ND (Tukey's test, $p < 0.05$).

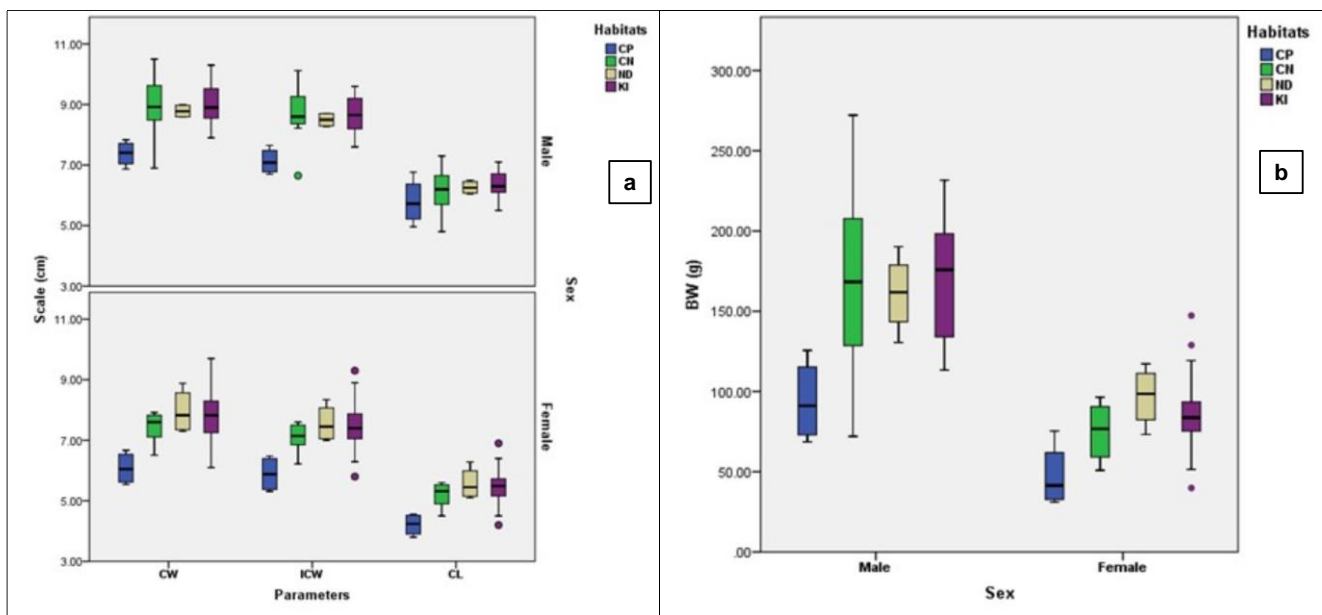


Figure 4 Proportion of size (CW, ICW, CL) (a) and body weight (BW) (b) variations in male and female *S. olivacea* mates across different habitats in the Bay of Bengal, Bangladesh (CP = Char Pataliya; CN = Char Nizam; ND = Nijhum Dwip; KI = Knife Island).

3.2.3. Seasonal influence

Significant seasonal variation was observed in CW, ICW, and BW for both males and females (t test, $p < 0.05$), except for the CL of males (t test, $p > 0.05$) (Table 4, Figure 5a-b). Larger CW, ICW, CL, and BW values were recorded during the rainy season than during the winter season for both sexes (Table 3). For male crabs, the mean CW, ICW, CL, and BW were 9.06 ± 0.57 cm, 8.72 ± 0.50 cm, 6.34 ± 0.44 cm, and 173.60 ± 36.28 g, respectively, during the rainy season and 8.11 ± 1.16 cm, 7.81 ± 1.12 cm, 5.92 ± 0.79 cm, and 129.65 ± 62.93 g, respectively, during the winter season. For females, the CW, ICW, CL, and BW were 7.87 ± 0.83 cm, 7.49 ± 0.75 cm, 5.47 ± 0.60 cm, and 87.82 ± 23.78 g, respectively, in the rainy season and 6.79 ± 0.92 cm, 6.51 ± 0.84 cm, 4.79 ± 0.73 cm, and 62.83 ± 24.70 g, respectively, in the winter season.

3.3. Molting

The average increase in newly molted *S. olivacea* was 1.28 ± 0.48 cm (CW), 0.93 ± 0.33 cm (CL), and 0.54 ± 0.19 cm (BH), with percentage increases of $22.00 \pm 5.56\%$, $25.32 \pm 8.80\%$, and $29.60 \pm 14.02\%$, respectively (Table 5). For *S. paramamosain*, the increments were 1.35 ± 0.18 cm (CW), 0.83 ± 0.15 cm (CL), and 0.45 ± 0.17 cm (BH), with percentage increments of $27.74 \pm 0.89\%$, $25.89 \pm 5.83\%$, and $26.91 \pm 13.06\%$, respectively. In *S. olivacea*, males presented slightly lower increases (CW: 1.08 ± 0.50 cm; CL: 0.90 ± 0.37 cm; BH: 0.50 ± 0.24 cm) than females did (CW: 1.38 ± 0.45 cm; CL: 0.94 ± 0.33 cm; BH: 0.56 ± 0.17 cm), with corresponding percentage increases reflecting a similar pattern. However, no significant differences were detected in the CW, CL, or BH increases between species (*S. olivacea* and *S. paramamosain*) or between the sexes of *S. olivacea* (t test, $p > 0.05$).

Regression analysis between premolt CW, CL, and BH and the increment revealed a significant positive correlation ($p < 0.01$), except for BH, which showed no significant relationship with increment ($p > 0.05$) (Figure 6a-c). Consequently, a

significant negative correlation was observed between premolt BH and the percentage of increase ($p < 0.01$), whereas premolt CW and CL exhibited nonsignificant negative correlations (Figure 6a-c).

Table 5 Range and mean values of carapace width (CW), carapace length (CL), and body height (BH) in premolt, postmolt, increment, and percentage (%) increments of two sympatric mud crabs, *S. olivacea* and *S. paramamosain*, from the coastal zone of Pattani Bay, Thailand.

Factors	Parameters	<i>S. olivacea</i>				<i>S. paramamosain</i>			
		Male (n = 6)	Female (n = 13)		Pooled (n = 19)		Pooled (n = 4)		
		Min–Max	Ave \pm SD	Min–Max	Ave \pm SD	Min–Max	Ave \pm SD	Min–Max	Ave \pm SE
Premolt	CW (cm)	4.00-6.50	5.01 \pm 1.10	4.10-9.13	6.16 \pm 1.86	4.00-9.13	5.80 \pm 1.71	4.30-5.96	4.89 \pm 0.74
	CL (cm)	2.20-4.17	3.18 \pm 0.80	2.20-6.28	4.11 \pm 1.39	2.20-6.28	3.82 \pm 1.29	2.91-3.89	3.24 \pm 0.44
	BH (cm)	1.18-2.45	1.69 \pm 0.53	1.28-3.36	2.19 \pm 0.79	1.18-3.36	2.03 \pm 0.74	1.48-2.10	1.74 \pm 0.28
Postmolt	CW (cm)	4.57-8.17	6.09 \pm 1.50	4.61-10.89	7.54 \pm 2.25	5.57-10.89	7.08 \pm 2.12	5.49-7.56	6.24 \pm 0.92
	CL (cm)	2.98-5.64	4.08 \pm 1.06	3.18-7.51	5.06 \pm 1.64	2.98-7.51	4.75 \pm 1.53	3.58-4.64	4.07 \pm 0.44
	BH (cm)	1.70-3.16	2.19 \pm 0.57	1.78-4.10	2.75 \pm 0.87	1.70-4.10	2.57 \pm 0.81	1.92-2.39	2.19 \pm 0.20
Increment	CW (cm)	0.57-1.67	1.08 \pm 0.50	0.51-2.28	1.38 \pm 0.45	0.51-2.28	1.28 \pm 0.48	1.19-1.60	1.35 \pm 0.18
	CL (cm)	0.54-1.54	0.90 \pm 0.37	0.46-1.66	0.94 \pm 0.33	0.46-1.66	0.93 \pm 0.33	0.67-1.00	0.83 \pm 0.15
	BH (cm)	0.20-0.74	0.50 \pm 0.24	0.35-0.82	0.56 \pm 0.17	0.20-0.82	0.54 \pm 0.19	0.29-0.68	0.45 \pm 0.17
% Increment	CW (cm)	14.25-34.46	21.08 \pm 7.71	12.44-28.22	22.42 \pm 4.58	12.44-34.46	22.00 \pm 5.56	26.85-28.96	27.74 \pm 0.89
	CL (cm)	18.62-37.56	28.46 \pm 9.08	16.72-50.00	23.86 \pm 8.64	16.72-50.00	25.32 \pm 8.80	19.28-32.26	25.89 \pm 5.83
	BH (cm)	9.01-52.54	23.19 \pm 18.11	14.29-55.63	28.41 \pm 12.39	9.01-55.63	29.60 \pm 14.02	13.81-43.87	26.91 \pm 13.06

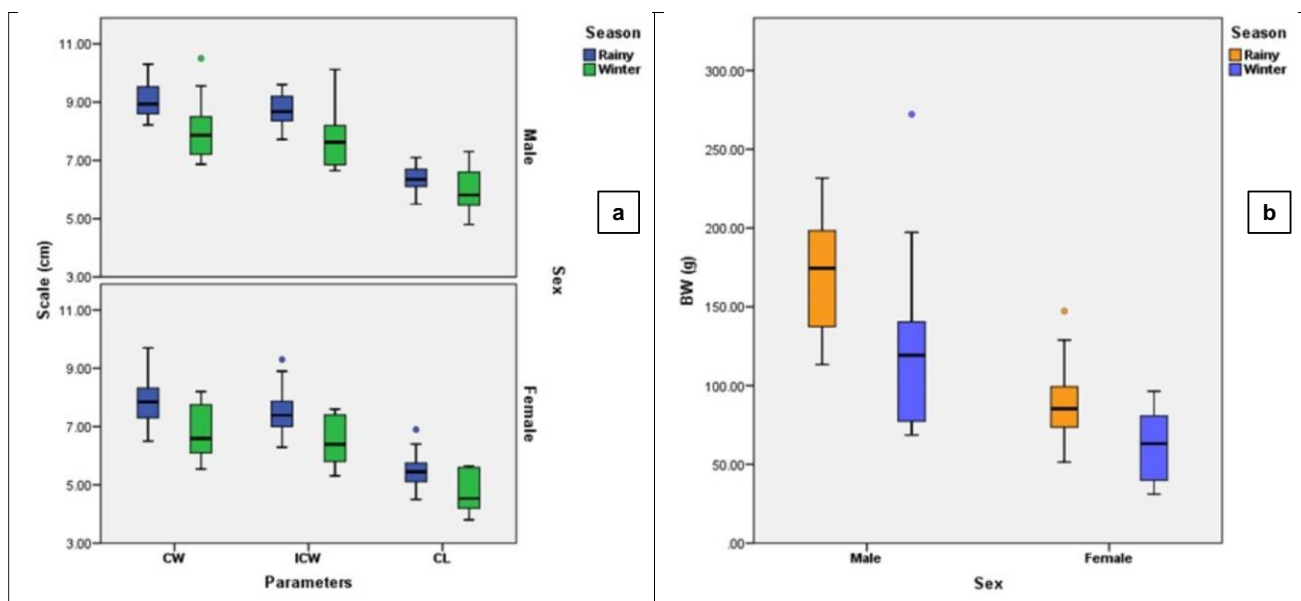


Figure 5 Size (CW, ICW, CL) (a) and BW (b) variation of male and female *S. olivacea* mates in the rainy and winter seasons in the Bay of Bengal, Bangladesh.

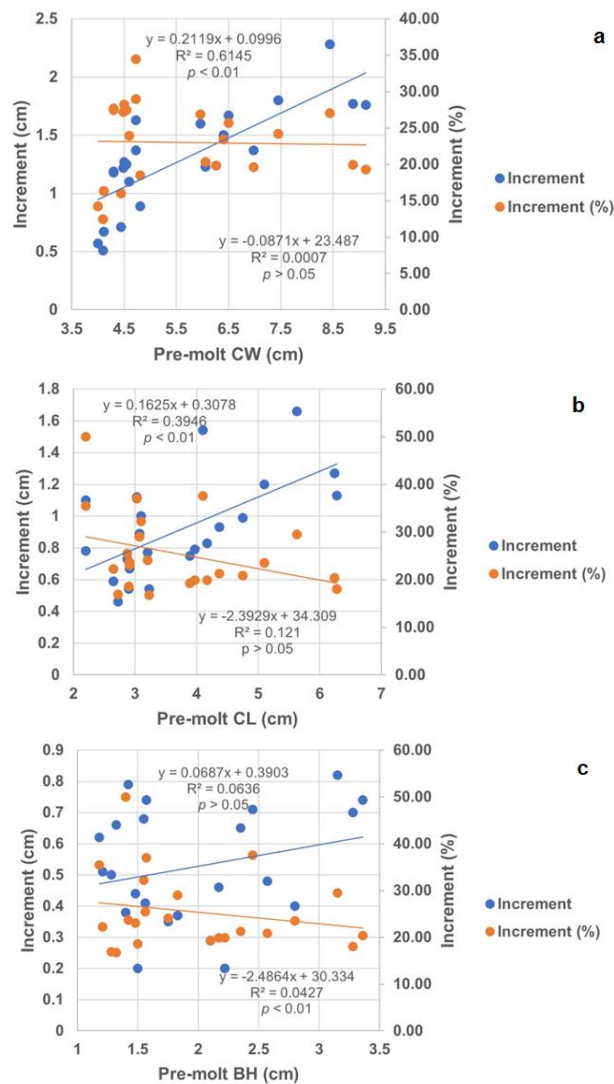


Figure 6 Correlations between body size (CW, CL, BH), increment, and percentage increment after molting in two mud crab species (*S. olivacea* and *S. paramamosain*) from the coastal zone of Pattani Bay, Thailand.

4. Discussion

Year-round breeding and recruitment of *Scylla* spp. have been documented in Bangladesh (Ali et al., 2020; Islam et al., 2024; Rahman et al., 2017; Rouf et al., 2021; Sakib et al., 2022; Zafar et al., 2006) as well as in other regions worldwide (Alberts-Hubatsch et al., 2016; Khaksari et al., 2023; Kumalah et al., 2017; Le Vay et al., 2007; Pati et al., 2023; Sara, 2010; Viswanathan et al., 2019; Zaidi et al., 2011). However, despite continuous reproductive activity, distinct seasonal peaks are evident. In Bangladesh, *S. olivacea* shows elevated breeding activity during March–April and August–October, corresponding to the pre-monsoon and monsoon seasons, respectively (Ali et al., 2020). Breeding and recruitment are highest during the monsoon (rainy) season and lowest in winter (Islam et al., 2024; Rouf et al., 2021).

In addition, rainfall was substantially higher during the rainy season (1800 mm) than in the winter season (37 mm), indicating that the abundance of *S. olivacea* mating pairs may be associated with rainfall patterns. Similarly, the abundance of *Scylla* spp. has been reported to be positively correlated with rainfall (Fazhan et al., 2017a). In the present study, higher species composition was also observed during the rainy season, which coincided with higher water temperatures (29.41 °C), whereas lower abundance occurred during the winter season with lower temperatures (22.36 °C). Likewise, a positive correlation between temperature and the abundance of *S. paramamosain* has been reported in the South China Sea (Fazhan et al., 2017a). Mud crab fisheries in Bangladesh have relied primarily on wild capture since the mid-1970s, with the rainy season representing the peak harvesting period (Rahman et al., 2017). Consequently, seasonal fluctuations in reproductive intensity directly influence crab availability in natural populations. The variation in sample size observed between seasons in the present study is therefore consistent with documented recruitment patterns.

Size-assortative mating was observed in *S. olivacea*, with 85% of males being larger than their female mates and 15% of pairs being larger females. This pattern aligns with previous studies in *Scylla* and other brachyuran crabs, where males typically

select smaller females to facilitate copulation, although occasional pairing with larger females also occurs (Clark & Backwell, 2016; Fazhan et al., 2017b; Tina et al., 2018; Tina & Muramatsu, 2020; Waiho et al., 2015). In Malaysia, wild and captive *S. olivacea* and other *Scylla* species (*S. paramamosain* and *S. tranquebarica*) are paired predominantly with smaller females (Fazhan et al., 2017b; Waiho et al., 2015). In addition, other brachyuran crabs, including *Austruca perplexa* (Tina & Muramatsu, 2020), *Austruca Bengali* (Tina et al., 2018), and *Grapsus depressus* (Fukui, 1995), also exhibit males that are larger than females during mate selection. Male preference for smaller females is generally associated with easier copulation and postcopulatory guarding (Fazhan et al., 2017b; Waiho et al., 2015). The occasional mating of larger females has been reported in *Uca mjoebergi* (Slatyer et al., 2012) and was observed at a low frequency in this study. Unlike fiddler crabs, which mate with hard-shelled females, *Scylla* crabs mate during the female molting phase, allowing increased female body size before copulation (Fazhan et al., 2017b). No significant differences in mating success were detected across male size classes, indicating that smaller males are equally capable of successful mating. These dynamics are likely mediated by female pheromone signaling and male receptivity, highlighting the complex interplay between body size, mating strategy, and reproductive success in *Scylla* mud crabs (Fazhan et al., 2017b).

In the present study, the highest mating frequency was recorded in males in the 8.5–9.0 cm size class and in females in the 7.5–8.0 cm size class in the Bay of Bengal (Figure 3). In contrast, *S. olivacea* from Malaysia exhibited peak mating at 10.0–10.9 cm for males and 9.0–9.9 cm for females (Ikhwanuddin et al., 2011). The size at first maturity has been reported to be 6.0 cm for both sexes in Malaysian mangrove forests (Ikhwanuddin et al., 2011), whereas mature females were observed at 7.0 cm in the Sundarbans mangrove forest, with underdeveloped ovaries also recorded at 5.0 cm (Ali et al., 2020).

The morphometric traits (length and weight) of male and female mates varied significantly across habitats in this study (Figure 4). The size at maturity and mating of mud crabs also differ with habitat conditions (Alberts-Hubatsch et al., 2016; Ali et al., 2020; Islam et al., 2025). For example, the size at first sexual maturity of *S. olivacea* was reported to be 6.88 cm for males and 6.59 cm for females in the Gulf of Thailand, whereas in the Andaman Sea, it was 6.38 cm for males and 6.58 cm for females (Islam et al., 2025). Similarly, *S. serrata* varies in size at maturity, with 6.1 cm recorded in both the Peel Harvey Estuary and Shark Bay and 8.4 cm in the Leschenault Estuary (Ali et al., 2020).

Mates of *S. olivacea* were significantly smaller during the winter and larger during the rainy season (Figure 5). Seasonal variation in river discharge and rainfall regulates salinity, temperature, and nutrient levels in coastal waters (Ali et al., 2020; Shaha et al., 2022). During the rainy season, maximum river discharge results in lower salinity, whereas minimum discharge in winter leads to higher salinity in the coastal areas of the Bay of Bengal, including the Meghna Estuary (Ali et al., 2020; Hossain et al., 2012; Shaha et al., 2022). Elevated salinity during the winter season has been reported to favor the maturation, reproduction, and spawning of mud crabs compared with the lower salinity conditions of the rainy season (Ali et al., 2020), which supports the findings of this study. Mud crabs exhibit thermoregulatory responses that influence their physiology, metabolism, and reproduction (Baylon, 2010; Fazhan et al., 2017a; Hidir et al., 2022; Liu et al., 2022b; Syafaat et al., 2021; Zeng, 2007). Temperature has been shown to affect growth, survival, and egg development in several *Scylla* species. For example, *Scylla paramamosain* exhibits lower growth and survival at lower temperatures (24 °C) and higher growth at 28 °C (Syafaat et al., 2021). Similarly, the egg incubation period of *S. serrata* decreased from 30 to 10 days as the temperature increased from 20.3 °C to 30 °C under captive conditions (Hamasaki, 2003). In addition, significant seasonal variation in carapace width has been reported in *S. tranquebarica* and *S. paramamosain* from wild populations in Malaysia, suggesting that environmental conditions influence body size (Fazhan et al., 2017a).

Besides temperature, salinity is another key environmental factor regulating mud crab physiology (Manimaran et al., 2025; Pati et al., 2023; Xu et al., 2023; Yao et al., 2021). Crustaceans expend considerable energy maintaining osmotic balance through ion regulation, and deviations from optimal salinity can increase metabolic costs and reduce growth performance (Pati et al., 2023; Xu et al., 2023; Yao et al., 2021). For instance, *S. serrata* showed higher osmoregulatory activity at 24 ppt compared with lower activity at 14 ppt in Taiwan (Pati et al., 2023). In the present study, smaller size mating pairs (lower CW and CL) were observed during winter when salinity was relatively higher (10.53 ppt) and temperature lower (22.36 °C), whereas larger crabs occurred during the rainy season with higher temperature (29.41 °C) and lower salinity (0.22 ppt) (Table 2). These patterns are consistent with previous studies suggesting that temperature and salinity jointly influence growth and physiological performance in *Scylla* species.”

Molting, or ecdysis, is a critical physiological process in the life cycle of crabs and involves the replacement of the old carapace with a new carapace to enable growth (Fazhan et al., 2017b; Fujaya et al., 2020; Serdiati et al., 2025). In this study, newly molted *S. olivacea* presented a mean increase of 1.28 ± 0.48 cm (CW), whereas *S. paramamosain* presented slightly greater increases of 1.35 ± 0.18 cm (CW) (Table 5). Comparable results have been reported in closed recirculation systems, where *S. olivacea* presented CW increases ranging from 6.3–14.43 mm (mean 8.8 ± 1.8 mm) and BW increases ranging from 20.2–38.2 g (mean 30.5 ± 4.9 g) (Serdiati et al., 2025). Similarly, Tahya et al. (2016) reported average increases of 10.58 mm (CW) and 30.13 g (BW) in postmolt *S. olivacea*, whereas *S. serrata* increased in CW from 15.33 ± 1.61 mm to 16.83 ± 0.76 mm (Nurcahyono et al., 2024). Previous studies further indicate that, compared with *S. paramamosain* (13.94 ± 3.12 mm) and *S. tranquebarica* (13.07 ± 2.12 mm), *S. olivacea* generally has lower growth increments (average = 11.50 ± 1.99 mm) (Fazhan et al., 2017b), which is consistent with our findings of lower increments in *S. olivacea* and greater increments in *S. paramamosain*.

Significant variation in postmolt increments was observed among *Scylla* species during the female mating cycle, although no differences were detected across size classes (Fazhan et al., 2017b). However, the percentage increase in CW was highest in smaller crabs of the three *Scylla* species (*S. olivacea*, *S. paramamosain*, and *S. tranquebarica*) and lowest in larger individuals (Fazhan et al., 2017b), which is consistent with our findings. In *S. olivacea*, males presented mean increases of 1.08 ± 0.50 cm (CW) and 0.90 ± 0.37 cm (CL), whereas females presented increases of 1.38 ± 0.45 cm (CW) and 0.94 ± 0.33 cm (CL). Similarly, the average increment of postmolt *S. olivacea* was 11.3 ± 2.6 mm and 10.5 ± 2.8 mm of CW, 7.7 ± 1.9 mm and 8.0 ± 2.1 mm of CL, and 36.1 ± 12.1 g and 37.6 ± 13.7 g of BW for males and females, respectively (Fujaya et al., 2020). Molting is regulated through distinct physiological stages, culminating in the release of the molting hormone ecdysone, which triggers shedding of the exoskeleton. During this process, crabs absorb water and minerals such as calcium to expand their body size before the new carapace hardens (Serdiati et al., 2025).

Molting is the primary biological process indicating growth in crustaceans, although it is often difficult to measure directly (Fatihah et al., 2017; Fazhan et al., 2017b; Islam et al., 2026; Kodama et al., 2005; Pati et al., 2023; Sanda et al., 2022; Serdiati et al., 2025). Molting frequency is generally higher during early developmental stages as individuals grow toward sexual maturity and gradually decreases with age (Islam et al., 2024; Kodama et al., 2005; Rouf et al., 2021). Growth parameters may vary both inter- and intra-specifically and are influenced by ecological niche, environmental conditions, biological variation, and disease outbreaks. Among environmental factors, temperature strongly regulates molting frequency and growth in mud crabs (Fatihah et al., 2017; Islam et al., 2026; Pati et al., 2023; Sanda et al., 2022; Serdiati et al., 2025). For example, juveniles of *S. paramamosain* were able to molt at 15.4 °C, whereas juveniles of *S. serrata* did not molt at 15.2 °C (Sanda et al., 2022).

Salinity is another key environmental driver influencing molting and growth in mud crabs (Pati et al., 2023; Xu et al., 2023; Yao et al., 2021). Ecological differences between sympatric *Scylla* species may therefore contribute to variations in molting and growth increments. For instance, *S. olivacea* generally prefers mangrove habitats with relatively stable conditions, and its abundance has not been strongly associated with environmental variables such as temperature, salinity, or rainfall. In contrast, *S. paramamosain* typically inhabits subtidal areas within fringing mangrove zones and shows stronger associations with environmental variability (Fazhan et al., 2022, 2017a; Koolkalya et al., 2016; Pati et al., 2023; Vay, 2001). These ecological and environmental differences between *S. olivacea* and *S. paramamosain* may partly explain the variation in molting and growth increments observed between species. However, environmental parameters were not recorded during the molting-related sampling in this study, which represents a limitation of the present work.

5. Conclusion

This study revealed that the peak mating activity of *S. olivacea* occurs during the rainy (monsoon) season, while mating frequency declines during the winter season. The observed seasonal pattern appears to be closely associated with biometeorological parameters, including higher water temperature, lower salinity, increased rainfall, and greater freshwater discharge during the monsoon period. In contrast, lower temperatures, higher salinity, and reduced rainfall during winter were associated with reduced mating activity. These findings suggest that biometeorological conditions play a key role in regulating reproductive timing in *S. olivacea*, and therefore, monitoring these environmental parameters may provide a useful tool for predicting peak mating periods in the Bay of Bengal. Therefore, understanding the relationships between biometeorological parameters, reproductive timing, and growth dynamics provides valuable insights for resource conservation, sustainable fishery management, and the development of effective hatchery and aquaculture strategies for mud crab species.

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6. Declarations

6.1. Ethical considerations

Ethical approval was granted by the PSU IACUC (Approval No. MHESI 68014/256; Ref. AI010/2023), and all procedures were conducted in compliance with national and international guidelines.

6.2. Use of artificial intelligence (AI)

The authors declare that the generative artificial intelligence (AI) tool [chatgpt.com] was used exclusively for language editing and/or grammatical improvement. The use of AI did not influence the scientific content, study design, data analysis, data interpretation, results, or conclusions of the manuscript. Full responsibility for the content remains with the authors.

6.3. Conflict of interest

The authors declare that they have no competing financial or nonfinancial interests.

6.4. Funding

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